

PREY-SIZE SELECTION IN NESTING MALE AND FEMALE COOPER'S HAWKS

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ABSTRACT. — The size and frequency of prey delivered by nesting Cooper's Hawks (*Accipiter cooperii*) were monitored throughout the nestling period at five nests on Lopez Island, Washington. Based on vocalizations during food exchange, we estimate that males captured 63% of the prey delivered to nests. Birds, primarily American Robins (*Turdus migratorius*) and California Quail (*Callipepla californica*), represented 85% of the prey captured by both males and females. The food niches of both sexes were similar as measured by maximum likelihood estimators of niche breadth and overlap. When the counts of prey delivered by males and females were adjusted for bias due to unequal observation time between years and differential hunting effort by the sexes, there were no significant differences between the sexes, nesting pairs, or prey size classes in the number of prey delivered to nests. These results and those of several other studies call into question the food-niche hypothesis as a comprehensive explanation for sexual size dimorphism found in many raptorial birds. Received 26 Apr. 1984, accepted 25 July 1985.

Several authors have proposed that sexual size dimorphism in raptors is advantageous because it allows prey-size partitioning between the sexes, and thus more efficient use of the food resource (Selander 1966, Storer 1966, Snyder and Wiley 1976, Newton 1979, Andersson and Norberg 1981). To test this hypothesis, we monitored the size of prey taken by five pairs of Cooper's Hawks (*Accipiter cooperii*) and compared the frequency of prey delivery based on prey size, nesting pair, and sex.

STUDY AREA AND METHODS

The study was conducted on Lopez Island off the northwest coast of Washington, where Cooper's Hawks nest in the absence of Goshawks (*A. gentilis*) and Sharp-shinned Hawks (*A. striatus*). Because the diets and habitat use of these three species overlap in areas where they coexist (Reynolds et al. 1982, Moore and Henny 1983, Reynolds and Meslow 1984), the absence of interspecific competition on Lopez Island may permit a greater opportunity for segregation of the diets of the sexes.

The activities of five nesting pairs were observed from blinds for 4–16 h every third day from early June through fledging in mid-July, 1978–1979. Observations of a sixth pair were terminated in 1978 following loss of its five nestlings to owl predation. Data for this pair are excluded from our analysis. We have assumed that observations of the five pairs are independent, including those at Nest C (Table 1) where the pair was observed during consecutive nesting seasons. This assumption is likely met if the turnover rate in the study population is similar to that Newton (1982) found in a population of European Sparrow Hawks (*A. nisus*).

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Prey items delivered to the nests were assigned size categories of 3–27 g (Class 1), 28–91 g (Class 2), and >91 g (Class 3). These represent groups 1–3, 4–6, and 7–18 of the cubic function series of Storer (1966). Whereas most large prey could be identified to species, smaller prey delivered to the nests were often plucked or decapitated, making their identification difficult. Juvenile prey were assigned to size classes corresponding to 90% of the adult weight for the species.

Most of the prey captured by males were delivered to the nest by the females after a food transfer involving characteristic vocalizations. Prey delivered by the female without such vocalizations were assumed to have been taken by her. Our data are biased if adults consistently transport larger prey to the nest but consume some of the smaller prey, a pattern documented for other avian species (Royama 1966, Root 1967, Taylor 1979). We have no evidence that such behavior occurred during this study.

In 1978 potential avian prey were censused using a modification of the line-transect technique described by Anderson (1972). One 400-m transect was established in each of the three common habitats (Douglas fir forest, pasture, and mixed-shrub edge) near each of the monitored nest sites. Transects were censused on two consecutive mornings during the early nestling period (weeks 1–3) and the early fledgling period (weeks 4–6).

In 1979 the three habitats were sampled in proportion to their relative areas as measured from aerial photographs within a circle with a radius of 2 km around each nest, the approximate spacing distance of nesting Cooper's Hawks in Oregon (Reynolds 1975). Transects with 20 stations spaced at 60-m intervals were censused in proportion to the availability of each habitat within the defined territory. To make the data comparable to that of 1979, the 1978 indices for each habitat were multiplied by the appropriate proportion each was represented within defined territories. Frequencies within prey size classes were evaluated with respect to nesting pair (territory) and sex using log-linear analysis (Fienberg 1977).

RESULTS

Both the sex of the bird making the capture and the size of prey taken were recorded for 224 of 286 prey delivered to the nests under observation (Table 1). Based on vocalizations or observations of the male delivering prey to the nest, we assumed that males captured 63% of these prey. Birds represented 85% of the identified prey ($N = 110$) (Appendix 1). American Robins (*Turdus migratorius*) and California Quail (*Callipepla californica*) comprised 52 and 47% of the identified prey captured by males and females, respectively.

The prey delivery data (Table 1) were biased because of differences in observational time between years (50% more at each nest in 1978) and in numbers of prey deliveries by the sexes (41% more by males). When the categorical data were adjusted for these biases, there was no significant difference in prey deliveries between nesting pairs ($\chi^2 = 2.0$, $df = 4$, $P = 0.73$), between sexes ($\chi^2 = 0.2$, $df = 1$, $P = 0.67$) or between prey size classes ($\chi^2 = 4.1$, $df = 2$, $P = 0.13$). No higher-order effects were significant.

As the abundance and proportional use of avian prey were known, we calculated electivity indices, which measure the ability (or preference) of a predator to capture a particular prey species (Lawlor 1980). These indices indicated that both males and females showed a preference for prey size

TABLE 1
NUMBER OF PREY CAPTURED BY NESTING PAIRS OF COOPER'S HAWKS, LOPEZ ISLAND,
WASHINGTON

Year	Terri- tory	Sex	Prey size class			Total
			1	2	3	
1978	A	Male	9 (24) ^a	19 (50)	10 (26)	38
		Female	4 (24)	9 (53)	4 (24)	17
	C	Male	9 (31)	11 (38)	9 (31)	29
		Female	6 (21)	9 (31)	14 (48)	29
1979	B	Male	13 (54)	10 (42)	1 (4)	24
		Female	6 (38)	4 (25)	6 (38)	16
	C	Male	8 (30)	16 (59)	3 (11)	27
		Female	6 (55)	4 (36)	1 (9)	11
	D	Male	11 (46)	9 (38)	4 (17)	24
		Female	2 (22)	3 (33)	4 (44)	9
		All males	50 (35)	65 (46)	27 (19)	142
		All females	24 (29)	29 (35)	29 (35)	82

^a Percent of total.

Classes 2 and 3 (Table 2). Using the measures developed by Petraitis (1979), with the modification for sample size developed by Smith (1984), we found extensive overlap of the food niche between the sexes ($G = 0.96$; minimum 0.52; maximum 1.0), although niche breadth was moderate for both sexes ($W = 0.54$ for males and 0.44 for females; minimum 0; maximum 1.0).

DISCUSSION

Of the several possible explanations for our failure to find evidence that male and female Cooper's Hawks partitioned the food resource during the nesting season, two merit discussion. As females rarely hunted during the first 3 weeks of the nestling period, food niche partitioning may have occurred only when both sexes hunted prey. There was no significant difference, however, in the prey-use patterns of males between the period when the female rarely hunted and when both sexes hunted regularly ($\chi^2 = 1.17$, $df = 1$, $P > 0.05$).

Another possibility is that prey-size partitioning did not occur because the population was not food stressed. Although it is difficult to make definitive statements regarding food stress, inferences can be made from an examination of food consumption rates and fledging success (Newton 1979). Under conditions of food abundance, total food consumption by raptors should increase during the nestling period and differ according to brood size. Under conditions of food scarcity, the rate of food delivery

TABLE 2
ELECTIVITY INDICES OF NESTING COOPER'S HAWKS, LOPEZ ISLAND, WASHINGTON

Prey size class	Proportional availability	Proportional use		Electivity index	
		Male	Female	Male	Female
1	0.77	0.36	0.30	0.47	0.39
2	0.18	0.46	0.34	2.56	1.89
3	0.04	0.19	0.36	4.75	9.00

should show little increase despite (1) the increase in demand associated with maturation or (2) differences in brood size.

Peak rates of food delivery for the 5 pairs observed during this study occurred when the nestlings were 4 weeks of age. Larger broods (4–5 young) received significantly more prey than broods with 3 young ($F = 11.0$, $P < 0.05$). The overall prey delivery rates, both in frequency (9.1 prey/nest/day), and in biomass (883 g/nest/day) exceeded those reported by Snyder and Snyder (1973) for nesting pairs of Cooper's Hawks thought to be food-limited. In addition, fledging success in this study (3.6 young/successful nest) was greater than that reported for other nesting populations of Cooper's Hawks (Craighead and Craighead 1956, Schriver 1969, Henny and Wight 1972, Reynolds 1975).

Although sex-related differences in diet have been documented for species of dimorphic raptors (Storer 1966, Schipper 1973, Opdam 1975, Snyder and Wiley 1976, Newton 1978), some nesting populations show no significant intersexual dietary differences (Schipper 1973, Balgooyen 1976, Snyder and Wiley 1976). The latter results, together with those of this study, suggest that intersexual prey-size partitioning is not a comprehensive explanation for the marked sexual size dimorphism found in many raptorial birds.

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APPENDIX 1

TOTAL NUMBER OF IDENTIFIED PREY DELIVERED BY NESTING PAIRS OF COOPER'S HAWKS,
LOPEZ ISLAND, WASHINGTON

Species	No. individuals
Birds	
American Robin (<i>Turdus migratorius</i>)	25
California Quail (<i>Callipepla californica</i>)	22
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)	6
Olive-sided Flycatcher (<i>Contopus borealis</i>)	5
Band-tailed Pigeon (<i>Columba fasciata</i>)	4
Red-breasted Nuthatch (<i>Sitta canadensis</i>)	4
European Starling (<i>Sturnus vulgaris</i>)	4
Brewer's Blackbird (<i>Euphagus cyanocephalus</i>)	3
Northern Flicker (<i>Colaptes auratus</i>)	3
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	3
Dark-eyed Junco (<i>Junco hyemalis</i>)	2
Unidentified flycatcher (<i>Empidonax</i> sp.)	2
Northwestern Crow (<i>Corvus caurinus</i>)	1
Chestnut-backed Chickadee (<i>Parus rufescens</i>)	1
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	1
Domestic chicken (<i>Gallus</i> sp.)	1
Hutton's Vireo (<i>Vireo huttoni</i>)	1
Unidentified Vireo (<i>Vireo</i> sp.)	1
Mourning Dove (<i>Zenaida macroura</i>)	1
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	1
Song Sparrow (<i>Melospiza melodia</i>)	1
Unidentified finch (<i>Carpodacus</i> sp.)	1
Mammals	
Townsend's Chipmunk (<i>Tamias townsendi</i>)	9
Domestic rabbit (<i>Oryctolagus cuniculus</i>)	4
Unidentified rat (<i>Rattus</i> sp.)	2
Deer Mouse (<i>Peromyscus maniculatus</i>)	2